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Ecological studies of collembolan population in a pine forest soil
II. Vertical distribution of Collembola

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With 4 figures

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1. Introduction

It is well known that in forest soils, the majority of Collembola are generally concentrated in the litter and humus layers (Agrell 1941, Bellinger 1954, Poole 1961, Tamura 1967, Niijima 1971). Within these layers, individual species shows a different vertical distribution. In a soil profile, decreasing size of soil cavities with increasing depth determines a range of distribution of individual species in relation to their body length (Haarløv 1960). Although this structure of habitats is a primary factor of the vertical distribution of Collembola which cannot burrow in order to penetrate into deep layers, temperature, humidity, other environmental factors and food affect the vertical distribution.

In this study area, the drought in summer has usually a marked effect in the population size of Collembola. The present investigation was undertaken to examine the vertical distribution of Collembolan populations and the effects of the desiccation of the surface layer on the vertical distribution. This work forms a part of an ecological investigation of Collembolan populations in a pine forest soil (Takeda 1973, 1976).

2. Study area

This study was carried out in a Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) forest in Kamigamo Experimental Station of Kyoto University. It is about 12 km north of Kyoto City (35°04′ N and 135°43′ E). The sampling plot is located at the ridge of a hill, about 130 m in altitude. Vertically, this forest can be divided into four layers, i.e. high canopy, scrub, field and soil layer. High canopy layer is over 4 meters in height, consisting of *Pinus densiflora* only. Scrub layer is 2—4 meters in height, consisting of *Chamaecyparis obtusa* Endl. Field layer is below 2 meters, consisting of evergreen and deciduous seedlings. Soil profile under this plot shows no well developed structure with no transition zone between the A layer and the B layer. The boundary between the A layer and the B layer is very sharp. The organic soil layer (A_0) consists of three layers i.e., the L-, F- and H-layer. The L layer is about 1 cm in thickness, consisting of pine needles and other fallen leaves. The F-layer is about 2—3 cm in thickness, consisting of partially decomposed littter with portions of plant structures still recognizable and rootlets. The H-A layer is very thin and about 0.5 cm in thickness. The B layer is below 3—5 cm depth.

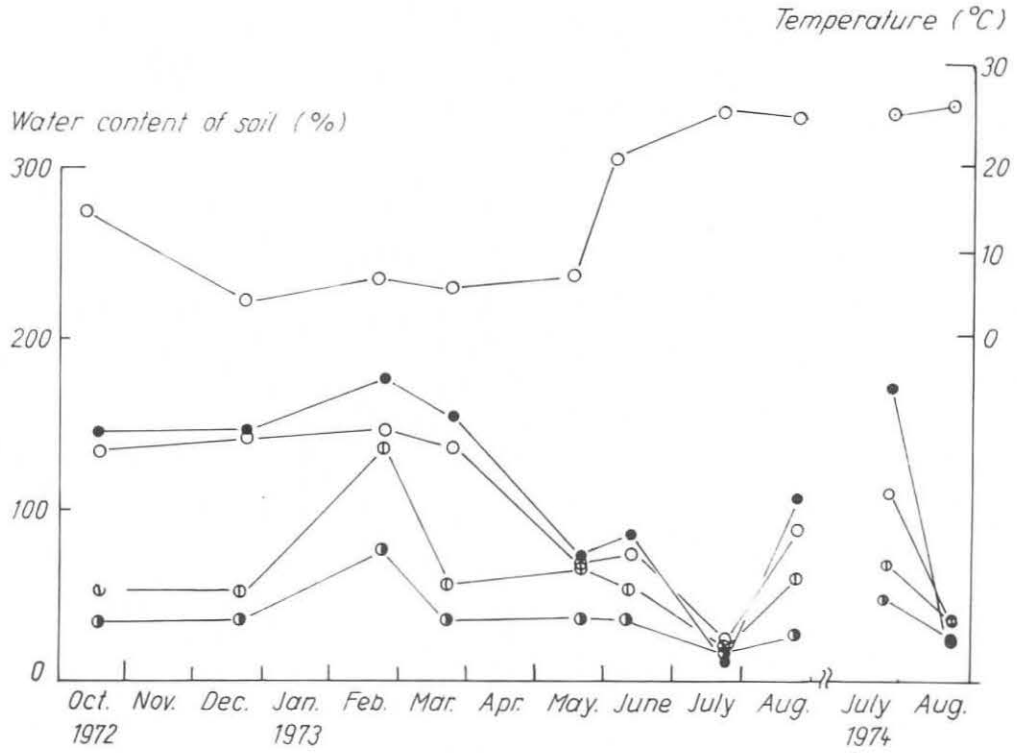

Fig. 1. Seasonal changes in the water content of soil and soil temperature at 2 cm deep during the study period. (●), (○), (◐) and (◑) indicate the soil water content in the 0—1, 1—2, 2—3 and 3—4 cm layer respectively: (○) indicates the soil temperature at 2 cm deep.

3. Sampling and extraction

A sampling plot was set up under the pine forest. This measured 10×10 m^2, being divided into 20 sub-plots of 1×5 m. Sampling was made on nine occasions between October 1972 and August 1973 and two further occasions, July 1974 and August 1974. On each sampling occasion, eight soil cores were taken from the plot. The soil cores were taken by using a soil sampler similar to that of MacFadyen (1961). In the laboratory, the soil core (4 cm in thickness and 25 cm^2 in area) was divided into four layers corresponding to the 0—1, 1—2, 2—3 and 3—4 cm layer. Each sub-core was 25 cm^2 in volume. On two sampling occasions July 1974 and April 1975, the sampling was extended to include the 4—8 cm layer, and the samples consisted of 20 and 15 soil cores respectively. Each soil core was 8 cm in thickness and 25 cm^2 in area (200 ml in volume).

On each sampling occasion, the soil temperature was measured with mercury in glass thermometers set at 2 cm deep at 2:00 p.m. The water content of soil cores was measured and expressed as the ratio of water to dry weight of soil.

4. Results

4.1. Seasonal changes in environment factors

Figure 1 shows the seasonal changes in the soil temperature at 2 cm below ground and water content of soil layer (0—4 cm). The low water content of the lower two layers may be due to the high mineral content of these layers. Although the estimations of water content of the four layers are not of comparable value, they indicate the degree of the seasonal changes in the water content of each layer. It can be seen that the water contents of the surface layer were very low during summer and the dry period was also the warmest part of year.

4.2. Vertical distribution of Collembola

Information concerning the vertical distribution to 8 cm depth was obtained from two series of samples taken on 26. July 1974 and 3 April 1975. The soil cores were taken to a depth of 8 cm and divided into two layers corresponding the 0—4 cm and 4—8 cm layer. The results are shown in table 1. and show that the majority of Collembola concentrated in the upper 0—4 cm layer. This concentration of individuals in the 0—4 cm layer is due

Table 1. Number of specimens (rel. number in italics) of different species collected at two dates in two layers

	26/VII/1974		3/IV/1975	
	0—4 cm	4—8 cm	0—4 cm	4—8 cm
Onychiurus decemosetosus Yosii	86	0	56	0
	(100)	*(0)*	*(100)*	*(0)*
Tullbergia yosii Rusek	489	53	983	49
	(90)	*(10)*	*(95)*	*(5)*
Tetracanthella sylvatica Yosii	60	6	292	105
	(91)	*(9)*	*(74)*	*(26)*
Folsomina onychiurina Denis	698	3	1133	21
	(100)	*(0)*	*(98)*	*(2)*
Folsomia octoculata Handschin	468	38	23	38
	(92)	*(8)*	*(38)*	*(62)*
Isotoma sensibilis (Tullberg)	112	2	56	0
	(98)	*(2)*	*(100)*	*(0)*
Isotoma carpenteri Börner	182	3	15	0
	(99)	*(1)*	*(100)*	*(0)*
Sinella dubiosa Yosii	49	5	9	1
	(91)	*(9)*	*(90)*	*(0)*
Tomocerus varius Folsom	80	0	25	0
	(100)	*(0)*	*(100)*	*(0)*
Oncopodura crassicornis Shoebotham	26	0	25	1
	(100)	*(0)*	*(96)*	*(4)*
Homidia sp.	55	1	—	—
	(98)	*(2)*		
other spp.	95	4	43	4
	(96)	*(4)*	*(92)*	*(8)*
Collembola (total)	**2400**	**115**	**2660**	**219**
	(95)	*(5)*	*(92)*	*(8)*
Number per 1 m²	48000	920	53900	4380

to the soil structure in this study area. Namely, below the A layer, the soil profile changes abruptly into the mineral soil layer which has a very compact structure. So Collembola are unable to penetrate below the organic layer, and the vertical distribution of Collembola is limited to the organic soil layer (A_0).

In order to examine the vertical distribution of Collembola in the A_0 layer, the soil samples to a depth of 4 cm were taken from the sampling plot during the period from October 1972 to August 1973, and additionally twice in summer 1974. In this study area, the depth of organic layer shows a heterogeneous distribution and ranges between about 1 cm and 5 cm in depth. Hence, the vertical distribution of the organic layer affects that of Collembola when the samples are randomly taken from the plot. The percentages of organic material in each layer were calculated from the frequency distribution of the depth of organic layer in the soil samples collected during the period of this study. The percentage of organic material in each layer is shown in Fig. 2. It is shown that the percentage of organic material changed from 100% to 27% with increasing depth. As the index of living space of each layer, the total porosity per volume of each soil layer was calculated from the sample data The results are shown in fig. 2.

If the individuals of each population are equally distributed throughout the organic layer, the pattern of vertical distribution of Collembola is the same as that of organic material. The comparison between the vertical distribution of each species and that of organic material is useful to detect the habitat selection of each species. The vertical distribution of 11 species and the Collembola as a whole are illustrated in Fig. 2. The statistical comparison (χ^2-test) of the number of individuals occurring in each layer and the theoretical number of individuels based on the percentage of organic material in each layer showed that all species examined and the Collembola as a whole did not equally distribute within the organic layer (f 3.

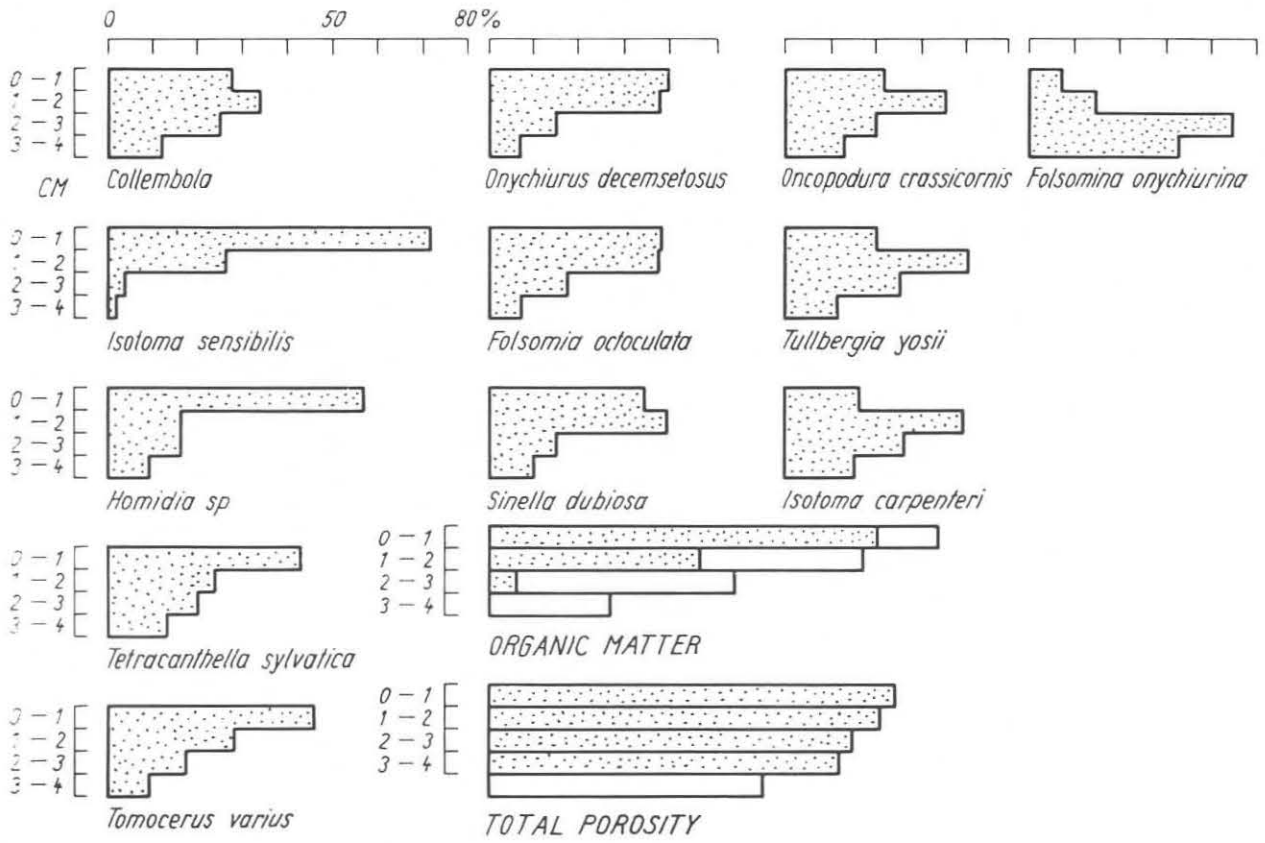

Fig. 2. Vertical distribution of Collembola, organic material and soil porosity. The number of Collembola in each soil layer is expressed as a percentage of the total populations. On the histogram of organic matter, diagnonal hatching, litter layer; white., F and H-A layers. The content of organic material and soil porosity in each layer are expressed as percentages of the total volume.

$P < 0.001$). The Collembola as a whole has its mode of vertical distribution at the 1—2 cm layer corresponding to the upper part of the F layer. Some morphological characters of each species are shown in table 2. According to the pattern of vertical distribution, the eleven species may be divided into four groups. The first group contains four species, i.e. *Isotoma sensibilis*, *Homidia* sp., *Tetracanthella sylvatics* and *Tomocerus varius*, and their distribution has a mode at the 0—1 cm layer corresponding to the litter layer. The second group contains three species i.e. *Onychirus decemosetosus*, *Folsomia octoculata* and *Sinella dubiosa*, distribution mainly over the 0—1 and 1—2 cm layer corresponding to the litter and the upper F layer. The third group contains three species, i.e. *Oncopodura crassicornis*, *Tullbergia yosii*, *Isotoma carpenteri*, having their mode of distribution at the 1—2 cm layer. The fourth group contains only one species, *Folsomia onychiurina* having its mode of distribution at 2—3 cm layer corresponding to the lower F layer and the H layer.

The vertical distribution of four species, i.e. *Folsomia octoculata*, *Folsomina onychiurina*, *Tetracanthella sylvatica*, *Tullbergia yosii* and the Collembola as a whole were studied in connection with the seasonal changes in water content and temperature. Fig. 3 shows the seasonal changes in vertical distribution of four species and the Collembola as a whole.

The degree of seasonal changes in vertical distribution of these species and the Collembola as a whole were expressed by the "mean depth" (M. D.) proposed by USHER (1969), as follows:

$$\text{M. D.} \quad \frac{0.5\,n_1 + 1.5\,n_2 + 2.5\,n_3 + 3.5n_4}{N}$$

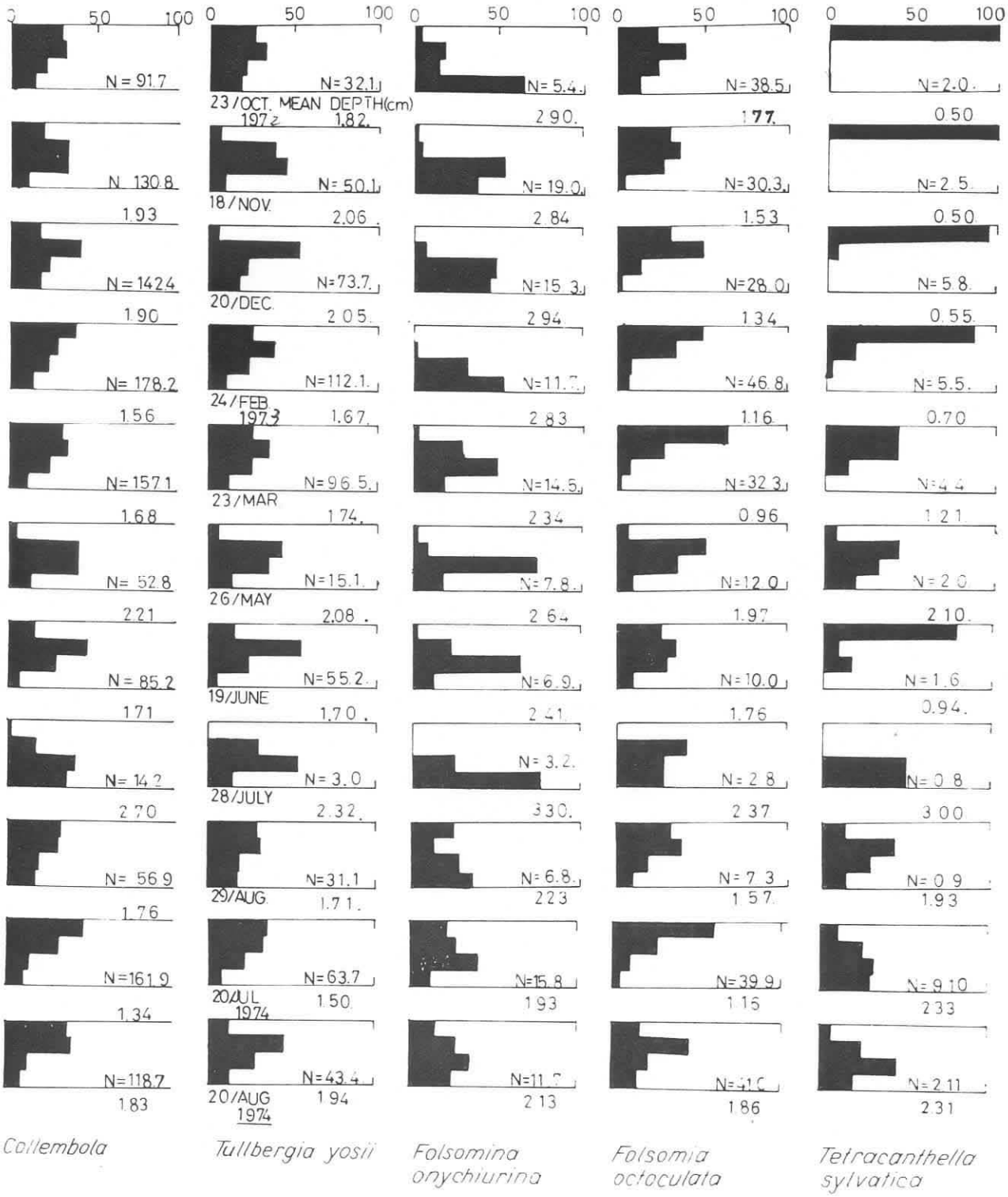

Fig. 3. Seasonal changes in vertical distribution of four species of Collembola and the Collembola as a whole. The number of Collembola in each soil layer is expressed as a percentage of the total population. Figures beside the histogram indicate the density per 100 cc soil core and the mean depth.

where n_1, n_2, n_3 and n_4 are the number of individuals in the 0—1, 1—2, 2—3 and 3—4 cm layer respectively and N is the number of individuals in all layers. The results are shown in Fig. 3. Using Kendall's coefficient of concordance ($W = 0.477$, $P < 0.05$), it is clear that the patterns of seasonal changes in vertical distribution show a significant degree of similarity among these species, so that the common pattern over four species can be expressed by a mean rank order value for each month and these values are plotted in fig. 4.

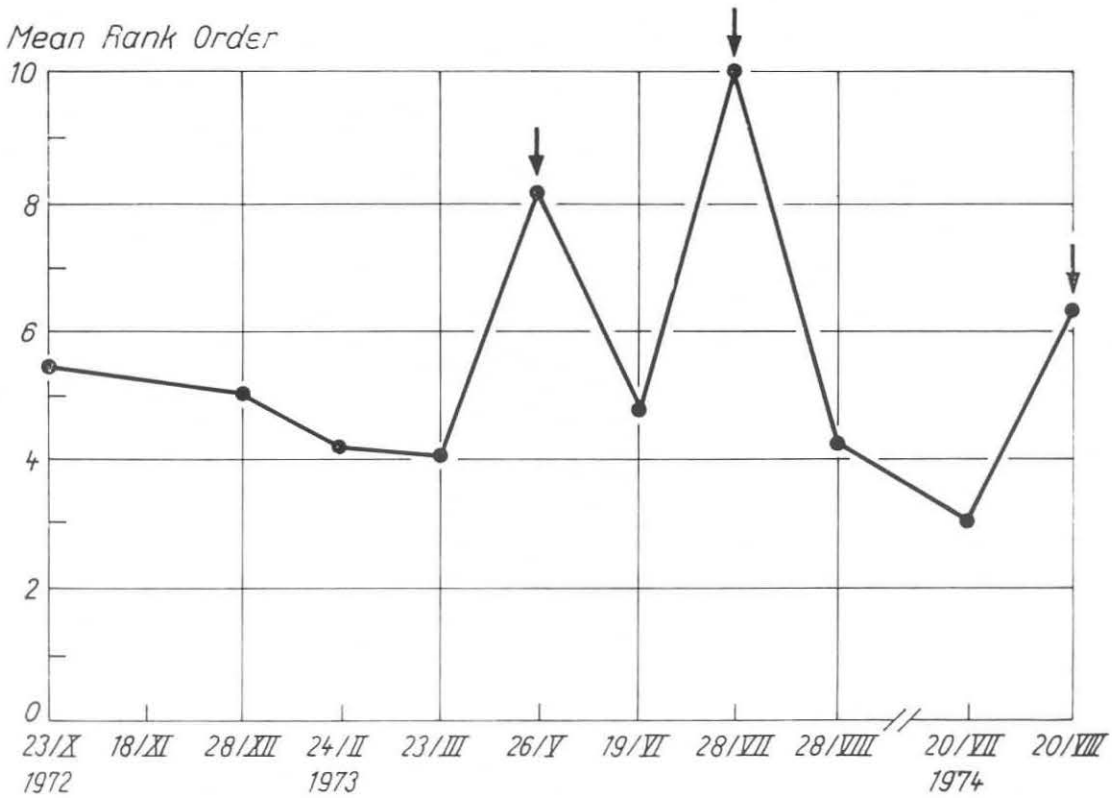

Fig. 4. Seasonal changes in mean rank order. Arrow indicates the occurrence of downward migration.

Table 2. Some morphological characters of 4 groups of collembolan species living in different strata of soil (I—IV)

species name	body length	eye	body colour	furca
I. (0—1 cm)				
Isotoma sensibilis	1.7 (mm)	+	+	+
Homidia sp.	2.5 (mm)	+	+	+
Tomocerus varius	2.1 (mm)	+	+	+
Tetracanthella sylvatica	1.3 (mm)	+	+	+
II. (0—2 cm)				
Onychiurus decemoculosus	0.8 (mm)	—	—	—
Folsomia octoculata	1.1 (mm)	+	+	+
Sinella dubiosa	1.5 (mm)	—	—	—
III. (1—2 cm)				
Oncopodura crassicornis	0.7 (mm)	—	—	+
Tullbergia yosii	0.5 (mm)	—	—	—
Isotoma carpenteri	2.5 (mm)	+	—	+
IV. (2—3 cm)				
Folsomia onychiurina	0.4 (mm)	—	—	—

Note. Symbols indicate the presence (+) or absence (—) of eye, body colouring and furca and species are ranked according to their mean depth of occurrence in the soil.

The relationship between body length and mean depth of occurrence was examined by using the Spearman rank correlation coefficient ($P = 0.63$; $P < 0.05$).

Table 3. Spearman rank correlation coefficients between the mean depth of occourrence of Collembola and the soil water content (at 0—1 cm) resp. the soil temperature (at 2 cm below ground)

	Temperature (P_r)	Water content (P_w)
Tullbergia yosii	0.206	0.758**
Folsomina onychiurina	-0.269	0.079
Folsomia octoculata	0.564*	0.867**
Tetracanthella sylvatica	0.745*	0.564*
Collembola **(total)**	**0.139**	**0.745***

Note. Significant at 0.01 (*) and at 0.05 (**).

There are three times of downward migration, i.e. May, July 1973 and August 1974. These times was accorded with the drought times and the high temperature in soil layer. To examine the factors affecting the seasonal trends of vertical distribution of these species, rank correlation coefficients between the mean depth and the water content of the 0—1 cm layer and the temperature at 2 cm depth were calculated. The results are shown in table 3.

It can be seen that the surface drought is significantly correlated with the mean depth of the Collembola as a whole. *Tullbergia yosii*, *Folsomia octoculata*, and *Tetracanthella sylvatica*. Against that, the temperature was significantly correlated with the mean depth of *Folsomia octoculata* and *Tetracanthella sylvatica*. Although the correlation of *Folsomina onychiurina* was not significant for both the temperature and the drought of the surface layer, a concentration of population in deeper layer was apparent under summer drought in 1973.

5. Discussion

As demonstrated in the present study, the majority of the populations occurred in the upper region of the soil profile. This agrees with the results of the other workers (Bellinger 1954, Poole 1961, Tamura 1967, Niijima 1971). In the present results, it may be seen that first: there is a correlation between body size of species and habitat selection, second, there is a correlation between morphological characters and habitat selection of species. Decrease of the size of pore space with increasing depth seems to be a limiting factor for the vertical distribution of the larger species such as *Tomocerus varius*, *Homidia* sp., *Isotoma sensibilis*, and *Sinella dubiosa*. The vertical distribution of the smaller species such as *Folsomia octoculata*, and *Tullbergia yosii* have their mode of vertical distribution over the F layer, and this suggests that the vertical distribution of the smaller species is related with other environmental factors rather than with the decrease of pore space.

In the larger species, *I. sensibilis*, *Homidia* sp. and *T. varius* which possess well developed eyes and pigment are abundant in the 0—1 cm layer and *I. carpenteri* and *Sinella dubiosa* possessing less eyes and less or no pigment are abundant in the 1—2 cm layer.

A similar zonation occurred among the humus dwelling forms, i.e. *Folsomia octoculata*, *Tullbergia yosii*, and *Folsomina onychiurina*.

Folsomina onychiurina occurred in the lower layers corresponding to the H-layer. This result was in accordance with Bellinger's observations on a population from a stand of young white pine forest in an old field area in U.S.A. (Bellinger 1954). *Isotoma sensibilis* was a typical surface dwelling form and Usher (1969) also found that this species had the mean depth usually laying between 1 ± 0.1 cm. *Tetracanthella sylvatica* showed a marked vertical migration throughout the course of post embryonic development. Although the changes in vertical distribution were similary affected by the environmental factor, as in the other species, the trend of migration suggests that an intrinsic behaviour is operative in the vertical migration (Takeda 1976).

Niijima (1971) observed that *Tomocerus varius* was a surface dwelling species and those results were in accordance with the present results.

The seasonal changes in vertical distribution of Collembola have been observed by some workers (Macfadyen 1952, Hale 1966, Usher 1969). In this study area, the vertical distribution of Collembola was affected by the seasonal changes in the surface water content of soil. The seasonal changes in vertical distribuation is usually explained by the vertical migration of animal or the vertical differential mortality. The vertical migration in response to drought occur when the water content of surface layer reaches the upper limits of desiccation tolerance of species of Collembola. In support of this view, Vannier (1970) showed that downward migration of Isotomidae took place as soon as the soil water potential reached a permanent wilting point for plants. Therefore, it may be reasonable to conclude that the surface drought of soil can cause the downward migration of Collembola. While the vertical differential mortality may be also important for the change of vertical distribution in the habitats where the ranges of living space of populations are physically limited by the soil structure.

The change in vertical distribution of *F. octoculata* and *T. yosii* and *Folsomina onychiurina* between June and July 1973 was accompanied by a rapid decrease in population size. It seems that the vertical differential mortality took place in these cases. The seasonal changes in vertical distribution are probably due to both the vertical differential mortality and the vertical migration. The downward migration to escape the unfavourable environmental conditions is important as a mean of survival for Collembola living under the changing environment.

6. Summary · Zusammenfassung

The vertical distribution of eleven species of Collembola and the Collembola as a whole was studied in a pine forest soil. All species of Collembola were more numerous in the top 3 cm of the soil layer corresponding to the L and F layers than in mineral soil layer. Within the organic soil layer, the vertical distribution of individual species was different among the species, relating to sheir morphological character and body size.

Seasonal changes in vertical distribution of four species groups and the Collembola as a whole were studied during the period of October 1972 to August 1973 in connection with the seasonal changes in soil water content and soil temperature. It was found that desiccation of the surface soil layer was an important factor, accounting for the seasonal changes in vertical distribution of the Collembola as a whole and three species of Collembola. The seasonal changes in soil temperature affected the vertical distribution of two species but not were related to those of the Collembola as a whole and the other species.

Colembolenbesatz in einem Kiefernforstboden. II. Vertikalverteilung der Collembolen

Die Vertikalverteilung von 11 Collembolenarten und der Collembolen insgesamt wurde in einem Kiefernforstboden untersucht. Alle Collembolenarten kamen in den oberen 3 cm (L- und F-Horizont) zahlreicher vor als im darunter liegenden Mineralboden. Innerhalb des O-Horizontes war die Vertikalverteilung der einzelnen Arten, in Übereinstimmung mit ihren morphologischen Merkmalen und ihrer Körpergröße, verschieden.

Jahreszeitliche Schwankungen der Vertikalverteilung von 4 Collenbolengruppen (d. s. Arten, die in den Schichten von 0—1, 1—2, 0—2 und 2—3 cm u. Fl. regelmäßig vorkamen) und des gesamten Collembolenbesatzes wurden in der Zeit vom Oktober 1972 bis August 1973 mit Rücksicht auf Schwankungen des Wassergehaltes (im O-Horizont) und der Bodentemperatur (in 2 cm Tiefe) untersucht. Dabei wurde gefunden, daß die Austrocknung der oberen Bodenschicht ein entscheidender Faktor für die jareszeitlichen Schwankungen der Vertikalverteilung der Collembolen insgesamt und von drei Arten war. Die jahreszeitlichen Temperaturschwankungen im Boden beeinflußten die Vertikalverteilung zweier Arten, nicht aber die der anderen Arten oder der Collembolen insgesamt.

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